

Selfish Sentinels in Cooperative Mammals

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Like humans engaged in risky activities, group members of some animal societies take turns acting as sentinels. Explanations of the evolution of sentinel behavior have frequently relied on kin selection or reciprocal altruism, but recent models suggest that guarding may be an individual's optimal activity once its stomach is full if no other animal is on guard. This paper provides support for this last explanation by showing that, in groups of meerkats (*Suricata suricatta*), animals guard from safe sites, and solitary individuals as well as group members spend part of their time on guard. Though individuals seldom take successive guarding bouts, there is no regular rota, and the provision of food increases contributions to guarding and reduces the latency between bouts by the same individual.

In some human societies, groups engaged in dangerous activities post sentinels who take watches according to an organized rota, each individual suffering the costs of guarding and then benefiting from a period of safety while other group members are on watch (1). Alternating guards or sentinels are also found in some social vertebrates (2–4), where individuals spend prolonged periods watching from raised positions, during which they are unable to feed (2). Several studies have shown that sentinels are usually the first individuals to detect approaching predators and often alert other group members to danger with their alarm calls (2, 3).

It is commonly suggested that sentinels suffer higher rates of predation than other group members (2, 3) and that coordinated guarding has probably evolved either through kin selection (5) or reciprocal altruism (6). Recently, Bednekoff (4) has pointed out that there is little evidence that sentinels are subject to increased risk of predation and has suggested that they may instead experience lower risks because they benefit from early detection of danger. If so, going on guard when no other individual is guarding may have immediate, direct benefits to individuals that have fed for long enough to be close to satiation. Simultaneous multiple guards may be uncommon because one guard is as effective as two or three, and resting rather than guarding becomes the optimal activity for satiated individuals once another animal is on

guard. The alternation of guarding between group members may occur because the benefits of feeding increase the longer an individual is on guard and decline the longer it has been foraging.

Bednekoff's model makes a number of predictions that differ from those of explanations of guarding behavior based on kin selection or reciprocal altruism. In particular, the costs of guarding should be low; solitary individuals (as well as those living in groups) should spend a proportion of their time guarding from raised positions; guarding should not be restricted to relatives; there should be no regular rotation of guarding duty; the probability that an individual will go on guard should be related to its nutritional status and to the amount of time for which it has been foraging; and individuals should respond to reduced contributions to guarding by other group members by raising the time that they themselves spend on guard.

This paper describes the pattern of guarding and tests these predictions in wild populations of the cooperative mongoose *Suricata suricatta* at our study site in the Kalahari Gemsbok Park, South Africa (7). Meerkats (or suricates) are diurnal desert-adapted mongooses living in arid areas of southern Africa (8). Groups (Fig. 1A) consist of 3 to 30 individuals that usually (though not invariably) include one dominant breeding female that is the mother of 75% of litters born in the group; a dominant male who fathers over three-quarters of the pups born in the group; 2 to 15 adult helpers of both sexes that assist in guarding, carrying, and feeding young; and a variable number of juveniles less than a year old (9, 10). Most subordinate adults are related to the breeding female, although some groups include more than one immigrant male that is unrelated to other group members.

The animals forage for 5 to 8 hours per day in the open, digging up to 20 cm below ground to reach invertebrates and small ver-

tebrates (11). While digging, they are unable to detect predators (Fig. 1B), which are common in the park, and annual rates of mortality are high (12). Digging animals frequently stop and glance around for short periods (Fig. 1C), an activity that we call "guarding away" (GA) (13). In addition, while groups are foraging, group members alternate in keeping guard from a raised position (GT) on a mound or a dead tree (13, 14) (Fig. 1D). Raised guards are present for about half the time that the group forages, and they alert other group members with graded alarm calls if predators approach (15). Guards announce their presence by repeated calls, and foraging animals are less vigilant when a guard is calling (15).

Guarding and Predation Risk

In groups living in the park, a raised guard was on duty for a median of 55.6% [interquartile range (IQR) 52 to 55.7%] of foraging time, and overall an adult spent 10.1% (IQR 9.0 to 10.3%) of group foraging time on raised guard (16). Raised guards spent most of their time looking away (17) from group members (Wilcoxon *T* test: $Z = 4.015$, $n = 20$ individuals, $P < 0.001$) (Fig. 2A) and gave alarm calls more frequently than did other group members (15). The calls alerted all other group members to danger and frequently caused them to run to the nearest burrow.

There was little evidence that individuals suffered increased risk of predation when on raised guard. During over 2000 hours of observation, no raised guards were attacked or killed by predators, probably because raised guards were usually the first to detect them (15). In addition, raised guards usually took up position within 5 m of a burrow (18), and on average were closer to safety than were foraging animals (paired *t* test: $t = 4.19$, $n = 14$ individuals, $P < 0.001$) (Fig. 2B). When predators approached, the guards were usually among the first animals below ground.

Our analysis compares the amount of time spent on guard in five groups in the park with similar measures for eight groups living on ranchland, where predators were less common (19). Raised guarding was more frequent in groups living in the park than in groups living on ranchland (Fig. 3). Groups on ranchland had a raised guard on duty for 12.0% of foraging time (IQR 9.3 to 14.1%), as compared to 55.6% in the park ($U = 0$, $n = 5$ or 8 groups, $P < 0.001$), and individuals spent a median of 1.5% (IQR 1.2 to 1.8%) of time on raised guard in ranch groups, as compared to 10.1% (IQR 9.0 to 10.3%) in the park ($U = 0$, $n = 5$ or 8 groups, $P < 0.001$). In contrast, time spent guarding at ground level (GA) and at burrow entrances (GB) did not differ between the two areas ($U = 16$, $n = 5$ or 8 groups, $P = 0.56$) (Fig. 3).

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Guarding and Group Size

The proportion of time that individuals spent on all types of guarding in the park increased in small groups ($F_{1,8} = 61.02$, $n = 10$ groups, $P < 0.001$) (Fig. 4A), as did the proportion of time spent on raised guard ($F_{2,6} = 8.14$, $n = 9$ groups, $P = 0.02$) (Fig. 4B). Solitary individuals and those in groups of two and three spent 12 to 22% of their time on raised guard (Fig. 4B), with the result that the proportion of time during which at least one individual was on raised guard was lower in small groups than in large ones ($F_{2,5} = 18.06$, $n = 8$ groups, $P = 0.005$) (Fig. 4C). Individuals in

small groups partly compensated for this by raising the amount of time that they spent being vigilant while digging ($F_{2,8} = 36.95$, $n = 11$ groups, $P < 0.001$) (Fig. 4D) but did not fully compensate (Fig. 4A). As would be expected, the mortality of adults increased as group size fell in both study sites (9).

Contributions to Raised Guarding

In most groups, all adult members typically contributed to raised guard, though individuals varied in their contributions (20). Across seven groups for which data were available, dominant females contributed significantly

less than other animals (Friedman test: $\chi^2 = 9.69$, $df = 3$, $P = 0.02$) (Fig. 5A). A multiple comparisons test (21) revealed no significant difference between other categories of adults. Immigrants that were unrelated to other group (22) members did not differ significantly in time spent on raised guard from individuals that were related to other group members (Wilcoxon signed ranks test: $T = 13$, $n = 7$ groups, $P = 0.5$) (Fig. 5B).

For the first 3 weeks after the birth of a litter, one individual in each group stayed at the burrow to “babysit” the pups for a day at a time, losing 1 to 2% of their body weight

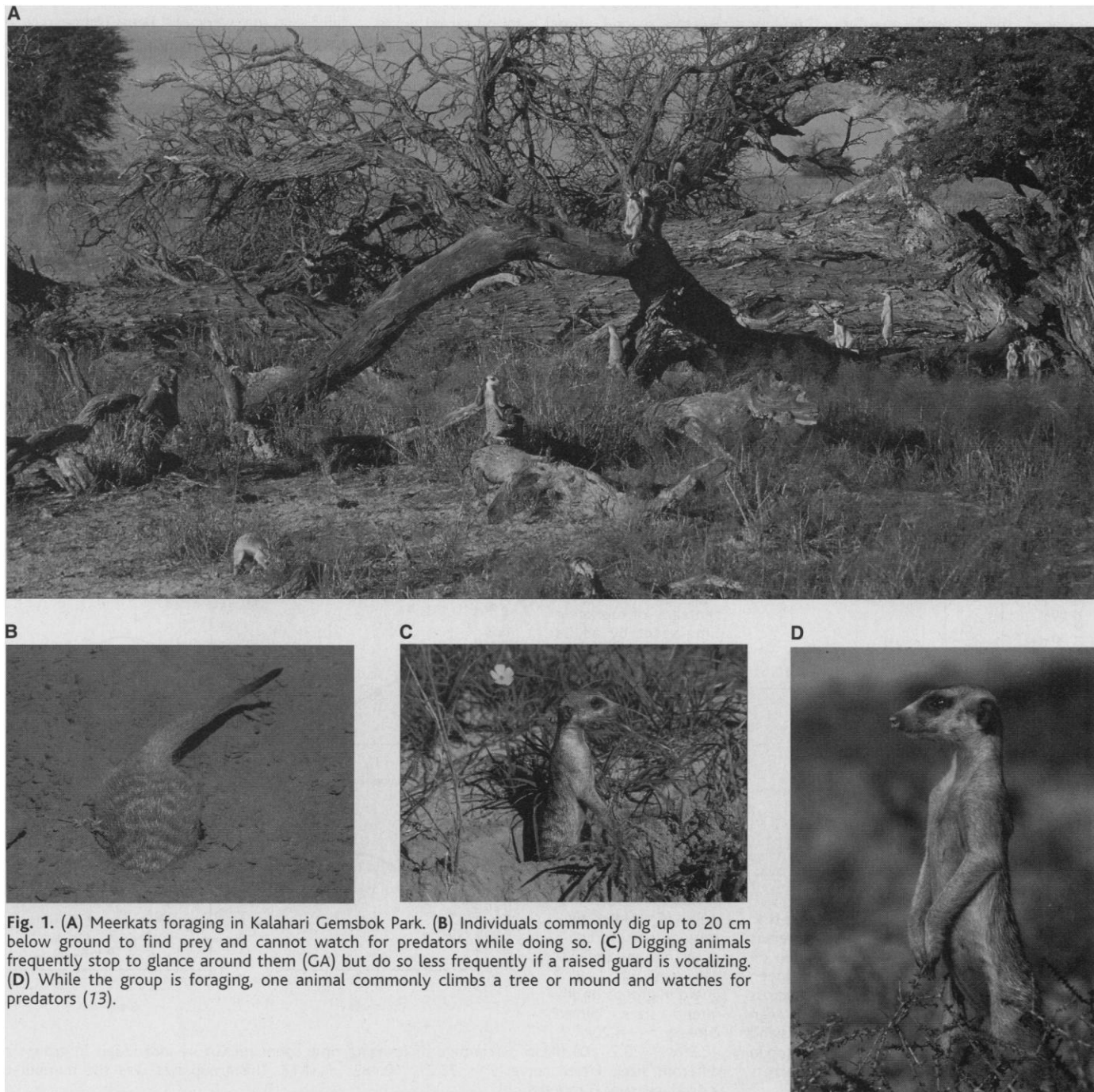


Fig. 1. (A) Meerkats foraging in Kalahari Gemsbok Park. (B) Individuals commonly dig up to 20 cm below ground to find prey and cannot watch for predators while doing so. (C) Digging animals frequently stop to glance around them (GA) but do so less frequently if a raised guard is vocalizing. (D) While the group is foraging, one animal commonly climbs a tree or mound and watches for predators (13).

per day spent babysitting (23). On the following day, individuals were consequently below their usual body weight and spent less time on raised guard than when they had spent the previous day foraging (Wilcoxon signed ranks test: $Z = 2.90$, $n = 21$ individuals, $P < 0.01$) (Fig. 5C), which suggests that guarding contributions might be related to the individual's nutritional status. To determine whether this was the case, we fed each of 10 group members with 25 g of hard-boiled egg at the start of one day, and their contribution to raised guarding over the rest of the day was compared to their average contribution to raised guarding on five previous days when they were not fed. Animals fed with egg increased their raised guarding time by around 30% (Wilcoxon matched pairs test: $T = 0$, $n = 10$ individuals, $P < 0.01$) (Fig. 5A) and spent more time in long (>60 s) guarding bouts ($T = 1$, $n = 10$ individuals, $P < 0.01$). In a subsequent experiment, half the subordinates ($n = 2$ to 6 animals) in six different groups were fed with 25 g of hard-boiled egg per day on 30 successive days, and their contributions to raised guarding were compared to those of controls matched for age and sex in the same group. Over the period of the experiment, fed animals showed an average weight gain of 82.6 ± 42.4 g of body weight, whereas controls gained 7.9 ± 51.6 g (paired t test: $t = 5.5$, $n = 6$, $P = 0.003$). Fed animals went on raised guard three times as often as did controls (Wilcoxon test: $T = 0$, $n = 6$, $P < 0.05$) (Fig. 6B). In addition, fed animals were more likely than were controls to go on raised guard before foraging each morning ($T = 0$, $n = 6$, $P < 0.05$) (Fig. 6C).

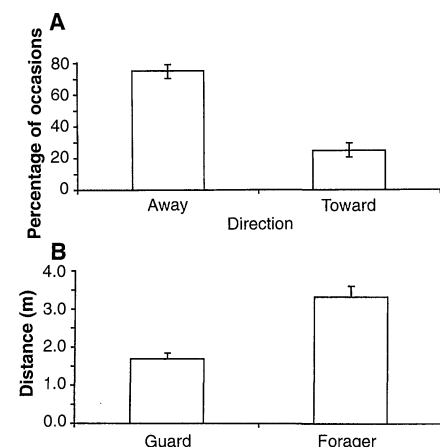


Fig. 2. (A) Median proportion of the time that 20 individuals spent looking toward versus away from foraging group members when on raised guard (16, 17). Median values (open bars) and IQRs (error bars) calculated across values for 20 individuals are shown. (B) Mean distance to the nearest bolt-hole for guards and foraging animals (18). Mean distances (open bars) and SDs (error bars) calculated across individual values are shown.

The extent to which feeding incremented raised guarding time did not differ between male and female helpers.

Alternation of Raised Guarding

Individuals alternated as raised guards (24). When raised guards returned to foraging, they were usually rapidly replaced by another group member, and the probability of an animal going on raised guard was approximately twice as high when no other animal was on raised guard as when a raised guard was already present (binomial test: $n = 7$ groups, $P < 0.02$; pooled $\chi^2 = 71.15$, $df = 1$, $P < 0.001$; but there is evidence of heterogeneity: $\chi^2 = 15.66$, $df = 6$, $P < 0.05$) (Fig. 7A). When a second animal went on raised guard while another was already guarding, one of the two usually terminated its guarding bout immediately.

The same individual rarely took two successive bouts of guarding, giving the superficial impression that guarding rotates among group members (25). However, individuals did not maintain a constant order of sentinel duty (15) and, although the same animal was less likely to take two successive bouts of raised guarding (pooled $\chi^2 = 11.44$, $df = 1$,

$P < 0.001$; heterogeneity test: $\chi^2 = 9.55$, $df = 5$, $P > 0.05$), individuals were as likely to resume guarding after one intervening bout as they were after several bouts (pooled $\chi^2 = 1.41$, $df = 1$, $P < 0.02$; heterogeneity test: $\chi^2 = 7.29$, $df = 5$, $P > 0.1$) (Fig. 7B).

If raised guarding alternated because the relative benefits of foraging versus guarding increased the longer an individual was on guard and declined with time spent foraging (4), the latency between guarding bouts by the same individual should be increased by shortening the duration of its guarding bouts or by provision of food. To determine whether this was the case, the average latency of uninterrupted guarding bouts by eight individuals was calculated, and (on average) 8 bouts (range, 6 to 10 bouts) by the same eight individuals were subsequently interrupted after they had been on guard for 2 min (26), and the latency from the interruption to their next bout of raised guarding was again measured (27). When raised guards were interrupted after 2 min, latency to the next guard declined from a median of 38.9 min for natural guarding bouts to 21.3 min for interrupted bouts (Wilcoxon signed ranks test: $T = 0$, $n = 8$, $P = 0.01$) (Fig. 8). When individuals were interrupted and fed with 25 g

Fig. 3. Time spent in three different categories of guarding by individuals in the Kalahari Gemsbok Park (open bars; $n = 5$ groups), where predators are abundant, versus on ranchland (striped bars; $n = 8$ groups), where predator numbers have been reduced (19, 20). GT, guarding from a raised position; GA, vigilant while foraging; GB, guarding at a burrow entrance (13). Open and striped bars show medians calculated across five groups in the park and eight groups on the farm; error bars show IQRs.

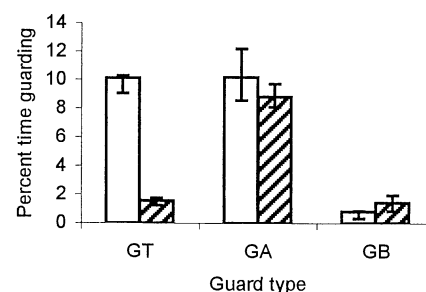
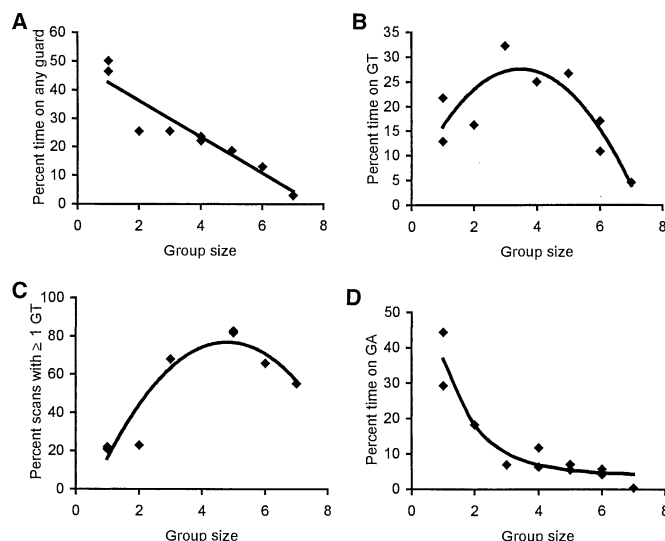


Fig. 4. (A) Mean percentage of foraging time spent by adults (>12 months old) on guard in groups of different sizes. Each diamond indicates a single group. The equation of the fitted line is $y = -0.138x + 7.23$. (B) Mean percentage of foraging time spent on raised guard by adults in groups of different sizes. Fitted curve: $y = -1.905x^2 + 13.25x + 4.51$. (C) Mean percentage of foraging time that any individual was on raised guard in groups of different sizes. Fitted curve: $y = -4.20x^2 + 40.39x - 20.2$. (D) Mean percentage of foraging time spent on GA by individuals in groups of different sizes. Fitted curve: $y = 75.2 \times 0.433^x + 4.17$. The group size was the number of individuals over 6 months old.



of hard-boiled egg (equivalent to their average morning weight gain), latency was further reduced to a median of 8.77 min (Mann-Whitney *U* test: $U = 9$, $n = 8$ experimental and 8 control individuals, $P < 0.02$) (Fig. 8).

Finally, our analysis investigated whether individuals showed any tendency to adjust the duration of their guards to the duration of guarding by other individuals. The mean duration of bouts of raised guarding over 6 days of observation was initially established for each of seven individuals. On one subsequent day, the duration of bouts of raised guarding by all other individuals in their group was restricted to 2 min by interrupting their bouts of raised guarding. This had no significant effect on the frequency with which interrupted animals or uninterrupted group members initiated guarding bouts (Wilcoxon signed ranks tests: interrupted animals: $T = 10$, $n = 8$ animals, $P = 0.26$; uninterrupted animals: $T = 10$, $n = 7$ animals, $P = 0.50$), but target

animals showed an increase in the average duration of their guarding bouts on these days (Wilcoxon signed ranks test: $T = 0$, $n = 7$, $P < 0.025$).

Our results support the assumptions and predictions of Bednekoff's (4) model of selfish sentinels: Guards inform all group members of the approach of potential predators; there is no evidence that individuals suffer increased risks of predation while they are guarding; solitary individuals spend amounts of time on raised guard that are similar to those spent by members of larger groups; and animals unrelated to other group members guard as much as do close relatives. However, although suricates may commonly gain immediate benefits by going on raised guard, other aspects of their behavior are difficult to explain without invoking either deferred direct benefits of some kind or kin selection. In particular, it seems unlikely that guards incur immediate direct benefits by giving alarm calls or by giving the "watchman's song" (15), though the costs of both are probably low.

Our results provide no indication that the alternation of raised guarding depends on social

processes more complex than the independent optimization of activity by individuals, subject to nutritional status and the presence (or absence) of an existing guard. Though individuals rarely take two protracted turns at raised guarding in succession, there is apparently no regular rota; guarding time is related to recent foraging success; the latency between guarding bouts by the same individual is shortened by curtailing the individual's previous guarding bout or by

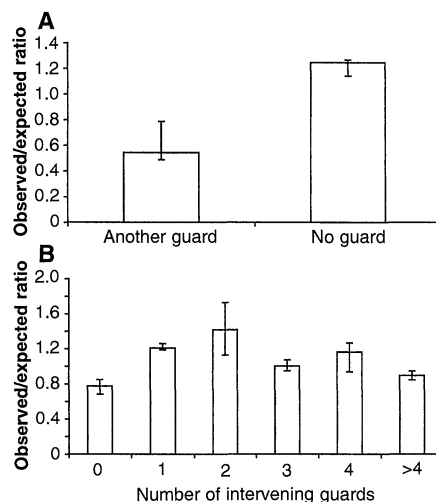


Fig. 7. Alternation of guarding. **(A)** The relative probability of individuals initiating raised guards in the presence or absence of another guard ($n = 7$ groups) (24). The median ratios of observed to expected frequencies in each state calculated across groups are shown (open bars) as well as IQRs (error bars); expected frequencies were calculated from the proportion of time that the group had a guard posted ("another guard") versus no guard. **(B)** The frequency with which individuals returned to raised guard after differing numbers of intervening guards, expressed as the ratio of the number of observed guard intervals to the frequency expected if the guard sequences were random (25). The median ratios are shown as well as IQRs calculated across groups; the analysis used two to five protracted guarding sequences from six groups; each sequence was collected over a single activity period and contained a mean of 35.8 guards (range, 10 to 99 guards).

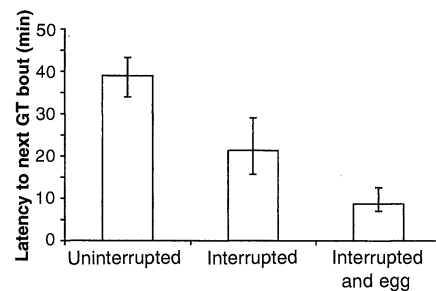


Fig. 8. Effects of shortening bout length and of feeding individuals on the latency to the next raised guarding bout by the same animal (26, 27). Sample size, eight individuals (27). Error bars indicate IQRs.

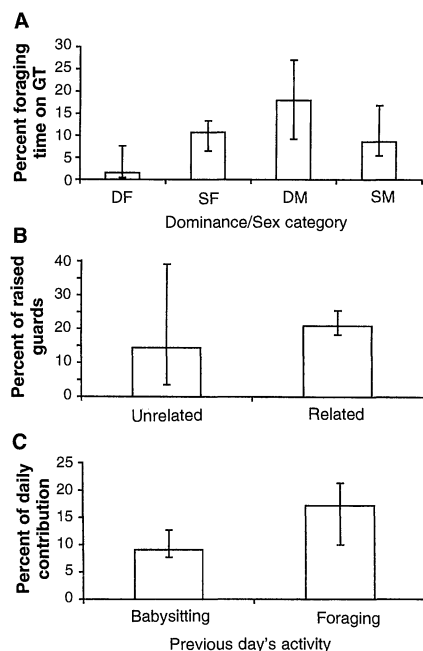


Fig. 5. **(A)** Median percentage of foraging time spent on raised guard by dominant (D) and subordinate (S) adults (M, male; F, female). Values shown in **(A)** through **(C)** are medians calculated across groups; error bars indicate IQRs (20). **(B)** Median percentage of foraging time spent on raised guard by immigrants unrelated to other group members versus time spent by adults related to the breeding female (mostly offspring or siblings). Unrelated individuals were identified from an analysis of knowledge of pedigrees combined with comparisons of genetic microsatellite markers (10, 22). **(C)** Median percentage of foraging time spent on raised guard by individuals on days when they had been babysitting on the previous day versus on days when they had been foraging on the previous day. The sample size in this case was 21 individuals drawn from six different groups.

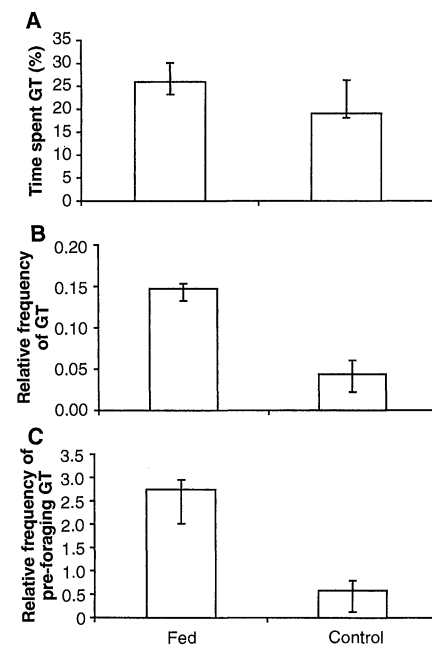


Fig. 6. **(A)** Contributions to raised guarding (percent of foraging time on raised guard) by 10 individuals on days when they had been fed with 25 g of hard-boiled egg (fed) as compared with the mean contribution to raised guarding by the same individuals on five previous days when they had not been fed (control). Open bars show median values calculated across individuals; error bars show IQRs. **(B)** Mean contributions to raised guarding by individuals in six groups fed each day over a 30-day period versus unfed controls in the same group. **(C)** Mean number of times fed and control individuals in six groups went on guard before starting to forage in the morning.

providing food; and individuals respond to reductions in guarding by other group members by increasing their own contributions. However, it is important to stress that evidence that the alternation of guarding among group members is a consequence of independent decisions provides no indication of the selection pressures maintaining guarding. This is because both an individual's nutritional status and the presence of existing guards might be expected to affect its optimal decisions in situations where guarding is maintained by kin selection or deferred benefits as well as in situations where guards gain immediate benefits themselves.

Our results differ in several respects from previous studies of coordinated vigilance in dwarf mongooses, where subordinate males are responsible for over 85% of all raised guarding (3). Here, sentinels act as a rear-guard while the group is moving and are frequently attacked and sometimes killed by predators when they leave their post and run to catch up with the group. One possible explanation of this difference is that, unlike dwarf mongooses, suricates live in a sandy environment where burrows are abundant, so that guards are usually close to a bolt-hole (Fig. 2B).

Finally, the pronounced difference in guarding behavior between groups living in the Kalahari Gemsbok Park (where predator numbers are high) and groups living on neighbouring ranchland (where predators have been reduced) suggests that learning plays an important role in the development of guarding behavior. We may need to recognize the possibility that although selection may favor an underlying predisposition to guarding, the distribution of guarding may be strongly influenced by the rewards that individuals experience from guarding during their own lifetimes. We should consequently not be surprised if the distribution of guarding across individuals fails to mirror the precise predictions of genetic models.

References and Notes

- Examples include lookout or sentry duty in fighting units, watch keeping by sailors, and supervision rotas in some industries.
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- Our study used a total of 18 different groups of meerkats, ranging in size from 2 to 20 adults, living within 50 km of Nossob in the Kalahari Gemsbok National Park (25°17'S, 20°32'E). The study area consisted of a mixture of dry riverbeds with river terraces on either side and sparsely vegetated sand dunes, and potential predators were abundant [see T. H. Clutton-Brock et al., *Afr. J. Ecol.* **37**, 69 (1999)].
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- A. S. Griffin, thesis, University of Edinburgh (1999).
- The principal foods of meerkats are beetles and their larvae, scorpions, solifugids, millipedes, and small lizards (8, 9).
- The main predators of meerkats are raptors (including martial eagles, tawny eagles, and bateleurs) and medium-sized carnivores (including black-backed jackals and African wild cats). Predators are abundant in the park, and annual rates of meerkat mortality are around 0.68 per year for adults (9).
- We identified three different categories of guarding: guarding from a raised position, usually a mound or a dead tree (GT), which individuals took in turn; guarding within 1 m of a burrow entrance (GB), which usually involved several animals at the same time and was a common response to an approaching predator; and guarding at ground level more than 1 m from a burrow entrance (GA), which involved short scans of the environment and was not coordinated among group members. Bouts of GT, GB, and GA differed in duration: The mean duration \pm SE of GT was 267.6 ± 74.9 s as compared to 109.3 ± 34.0 s for GB and 20.2 ± 1.41 s for GA ($F_{2,10} = 7.16$, $n = 6$ groups, $P = 0.01$).
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- We measured the amount of time that different individuals spent on raised guard (GT) as well as the amount of time they spent guarding at burrow entrances (GB) and the amount of time they were vigilant while foraging (GA) in five different groups in the park. All animals in our study groups could be recognized individually and were habituated to observers walking in the middle of the group. Except when predators approached or during the heat of the day, when they rested below ground, the animals spent most of their time foraging in the open, and it was usually possible to keep all individuals in view. Individuals were sexed during capture or by close observation and were classified as pups from 0 to 3 months of age, as juveniles from 3 to 12 months, and as adults at 12 months and over. The time spent guarding was estimated by scanning all group members at 10-min intervals and recording their activity on handheld computers during observation periods and was expressed as a percentage of group foraging time (periods when at least 75% of group members were foraging). In practice, activity was closely synchronized among group members, and (with the exception of sentinels) usually either all or no group members were foraging.
- A guard was recorded as looking toward the group when the group fell within 180° of its direction of gaze. The time spent looking toward versus away was sampled by recording the direction of gaze of guards at 10-min intervals. The proportion of time each individual spent looking toward versus away was calculated using an average of 46 scans per individual.
- Distances were sampled by recording the distance to the nearest bolt-hole whenever individuals went on raised guard and also by recording the same distance for a randomly identified foraging adult. An average of six records were collected for each of 14 individuals (range, 3 to 11 records per individual).
- Our second study area was close to Vanzylsrus, approximately 150 km southeast of Nossob, where we monitored the behavior of individuals in eight different groups. Here all predators except goshawks were less abundant, and annual rates of mortality were around 0.34 for adults (9).
- For each group, we calculated the percentage of foraging time spent on raised guard by each individual on at least 5 days. Where more than one subordinate of each sex was present in a group, means were calculated across individuals of the same sex to compare with values for dominant males and dominant females in the same group.
- J. H. Zar, *Biostatistical Analysis* (Prentice-Hall, London, 1996).
- Unrelated immigrants were identified by a knowledge of pedigrees combined with analysis of genetic microsatellite markers (10). Though we were only able to compare related and unrelated individuals in seven groups, the results of this comparison coincide with more extensive analyses of individual contributions to babysitting and other cooperative activities.
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- To investigate the alternation of guarding bouts, we recorded the start and end time and the type of every guarding bout over a 5-day period for each of seven groups. To investigate the effect of the presence of a raised guard on the frequency of raised guarding by other group members, we scored whether each raised guard was initiated during the presence or absence of another guard. We then compared these observed frequencies with expected frequencies, calculated from the proportion of the groups' foraging time during which at least one guard was present and controlling for the fact that fewer individuals were available to initiate guards when one animal was already on guard.
- We investigated patterns in the order in which individuals performed raised guards within each group by recording the number of intervening guards between consecutive guards by the same individual. We then compared the observed distribution of guard intervals with expected distributions calculated by randomizing each sequence 1000 times.
- As well as recording the distribution of guarding times, we were able to curtail individual guarding bouts by gently shaking the branch on which the animal was standing until it descended and started to forage again. Animals rarely attempted to return to raised guard immediately but, if they did so within a minute of ceasing to guard, we repeated the process until they desisted. In addition, to investigate the effects of nutrition on guarding, we fed some individuals with hard-boiled egg, comparing their behavior with that of unfed controls of similar age and sex.
- Uninterrupted guarding bouts: For eight individuals, we calculated the mean latency from the end of a period of uninterrupted raised guarding to its return to guard, for an average of 14 bouts per individual. Only periods of raised guard lasting at least 30 s were included, and samples were restricted to guarding bouts in the first half of the morning feeding period. Interrupted guarding bouts: Each individual in this sample was interrupted after guarding for 2 min on an average of eight occasions, and the mean latency to the individual's next return to guarding duty was calculated for these bouts. Interrupted and egg: We subsequently interrupted each individual once and fed it with 25 g of hard-boiled egg and again measured the latency to its next return to raised guard. Eight individuals were sampled one to three times each.
- We are grateful to the National Parks Board of the Republic of South Africa for permission to work in the Kalahari Gemsbok Park. For help and support we thank E. le Riche and D. Engelbrecht, wardens of the park; P. Novellie; A. Hall-Martin; D. Ras; J. Herrholdt; G. de Kock; S. de Waal; and Mr and Mrs H. Kotze for permission to work at Vanzylsrus. The study would not have been possible without the support of members of the Mammal Research Institute of the University of Pretoria, including J. Skinner, P. Richardson, A. MacKenzie, M. Haupt, and G. van Dyk. For access to genetic analyses, we are grateful to J. Pemberton and T. Marshall (Institute of Cell, Animal and Population Biology, University of Edinburgh). Thirty-five assistants contributed to data collection: G. Avey, J. Barnard, C. Britten, J. Chadwick, P. Chadwick, S. Clarke, P. Novellie; A. Hall-Martin; D. Ras; J. Herrholdt; G. de Kock; S. de Waal; and Mr and Mrs H. Kotze for permission to work at Vanzylsrus. 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